Life history matrices for TOSSM model

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The goal of this exercise was to devise a set of life-history matrices appropriate for use in the Testing of Spatial Structure Methods (TOSSM) model. These matrices should reflect the life history of a 'typical' baleen whale. The two species for which the most life history data are available are humpback whales and eastern pacific gray whales. We chose to base the TOSSM demography on that of the gray whale because its age at first reproduction (5-11 years; Reilly, 1984) is more typical of baleen whales than that of the humpback whale (4-5 years; Evans 1984).

We used the vital rate estimates for gray whales to parameterize stage-based matrices for use in the TOSSM model. We constructed matrices representing vital rates both at carrying capacity and near zero population density. Density dependence can be implemented by interpolating between these matrices.

Vital Rate Estimates at Carrying Capacity

Reilly (1984) reviewed vital rate estimates for eastern pacific gray whales and used them to construct an age-based Leslie matrix model. As no reliable estimate was available for juvenile mortality (S_j), he estimated S_j by fixing all other parameters and adjusting S_j to achieve a value for λ consistent with the observed rate of increase for the population. Following this method, we estimated juvenile survival at carrying capacity by holding all other parameters fixed and adjusting S_j to produce zero population growth.

Table 1. Vital rates for eastern Pacific gray whales. The first column shows the estimates used by Reilly (1984). The second column includes the pregnancy rate estimate from Perryman et al. (2002) and a juvenile survival rate adjusted to produce zero population growth. The third column shows the assumed biological limits that would be approach near zero population density.

Vital Rate	Estimate used by Reilly	Estimate at K	Value assumed near zero density
Juvenile survival*	0.893	0.92	0.940
Adult female survival	0.946	0.946	0.946
Adult male survival	0.954	0.954	0.954
Age of first reproduction	8 (5-11)	8 (5-11)	5
Pregnancy rate	0.463	0.24	0.5
λ	1.011	0.997	1.068
Generation Time	19.4	19.4	16.9

*Juvenile survival rate was not empirically estimated, but rather was derived fixing all other vital rates and adjusting to produce the desired value for λ.

Reilly's analysis used the pregnancy rate estimate of Rice and Wolman (1971) of 0.463. Perryman et al. (2002) recently published an estimated pregnancy rate of only 0.25[1]. Perryman et al.'s estimate, unlike that of Rice and Wolman, was made during a time when the population was believed to be at or near carrying capacity. Thus, that is the pregnancy rate estimate we used when the population is at carrying capacity.

Vital Rate Estimates Near Zero Density

To estimate the maximum rate of increase for eastern Pacific gray whales, Reilly identified the biological limits that their vital rates would approach as the population neared zero density (Table 1). We used these values to parameterize the stage-structured model near zero density.

Stage-Structured Model

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[1] Perryman et al. estimated that females with newborn calves comprised 6% of the population during the northbound migration. Adult females represent approximately 25% of the population at stable age distribution, implying a pregnancy rate of 0.06/0.25 = 0.24.

We used the above vital rates to construct a stage-based matrix for use in the TOSSM model. We defined five life-history stages: juvenile1, juvenile2, fertile female, lactating female and adult male (Figure 1). The use of two juvenile stages allowed better control of the average age at first reproduction (AFR). The juvenile1 stage corresponds to animals too young to have reached sexual maturity, while the juvenile2 stage represents animals that are old enough that they could mature and move into an adult stage class in the next time step. The use of separate fertile and lactating stages for adult females allowed enforcement of a minimum 2 year inter-birth interval.

We used the above vital rates to parameterize the stage-based matrix using a fixed stage duration model (Caswell, 2001). More sophisticated models are available (e.g., variable stage duration, negative binomial stage durations), but require estimates of the variance of the time spent in each stage, which are not available.

Table 2 shows the survival rates and durations used for each stage, both at zero population density and at carrying capacity. The average durations of the juvenile1 and juvenile2 stages were adjusted to produce the appropriate AFR for the two matrices, while the average duration of the fertile female stage was adjusted to vary the pregnancy rate. Since survival/growth occurs before reproduction in the model and since the lactating female class has a fixed duration of one year, every individual in the lactating female class will have just given birth to a calf. Therefore, the fertility rate for that class was set to 1.0.

Table 2. Estimates of survival rate (σ_i) and duration (T_i) for each stage and the resulting parameter estimates for the fixed stage duration model. γ_i is the proportion of individuals in stage i that move into the next stage each year. P_i is the probability of an individual surviving and remaining in stage i, while G_i is the probability of an individual surviving and moving into the next stage. F_i is the fertility rate for stage i.

Stage	σ_i	T_i	γ_i	P_i	G_i	F_i
Near zero population density:						
Juvenile1	0.94	4	0.223	0.73	0.210	0
Juvenile2	0.94	1	1	0	0.94	0
Fertile female	0.946	1	1	0	0.946	0
Lactating female	0.946	1	1	0	0.946	1
Adult male	0.954	-	-	0.954	-	0
Near carrying capacity:						
Juvenile1	0.92	6	0.134	0.797	0.123	0
Juvenile2	0.92	4	0.220	0.718	0.202	0
Fertile female	0.946	3	0.315	0.648	0.300	0
Lactating female	0.946	1	1	0	0.946	1
Adult male	0.954	-	-	0.954	-	0

The resulting matrices are shown in Table 3. Males and females are undifferentiated prior to sexual maturity. When an individual from the juvenile2 stage class matures, it has an equal probability of moving to the fertile female and adult male stages. The rates of increase (λ), generation times, pregnancy rates and proportion of the population in the lactating female stage-class resulting from these matrices are in close agreement with the age-based model (Table 4).

At the TOSSM workshop, it was agreed that in the initial phase of the project, the maximum sustainable yield rate (MSYR) for the TOSSM model should be approximately 4% (IWC 2003). The MSYR for the life tables below is approximately 3.5%. While this value differs slightly from what was specified at the workshop, the tables below have the advantage of being based on actual data, which seems preferable to altering the values in order to achieve a pre-specified MSYR.

Table. 3. Stage-based matrices for use at a) zero population density and b) carrying capacity. Stage class abbreviations are juve1 = juvenile1, juve2 = juvenile2, fert = fertile female, lact = lactating female, and male = adult male.

a)	juve1	juve2	fert	lact	male
juve1	0.730	0	0	1.0	0
juve2	0.210	0	0	0	0
fert	0	0.47	0	0.946	0
lact	0	0	0.946	0	0
male	0	0.47	0	0	0.954

b)	juve1	juve2	fert	lact	male
juve1	0.797	0	0	1.0	0
juve2	0.123	0.718	0	0	0
fert	0	0.101	0.648	0.946	0
lact	0	0	0.300	0	0
male	0	0.101	0	0	0.954

Table 4. Comparison of the age-based and stage-based matrices at zero population density and at carrying capacity. Generation time is defined as the average age of the mothers of a cohort. For the stage-based matrices, pregnancy rate is defined as the proportion of adult females that are in the lactating stage class, while % lactating is the proportion of the total population that is in the lactating female stage class.

	Zero Population Density		Carrying Capacity	
	Age-based	Stage-based	Age-based	Stage-based
Rate of increase (λ)	1.068	1.072	.997	0.998
Generation time	16.9	17.1	19.4	20.0
Pregnancy rate	0.5	0.47	--	0.23
% lactating	--	0.13	0.06	0.06

Implementing Density Dependence

The life-history matrices near zero population density and carrying capacity differ with respect to juvenile survival rates, mean AFR and mean inter-birth interval. The entries in the two stage-based matrices represent the two extremes of the spectrum. Thus, density dependence can be implemented by varying the entries in the life history matrix linearly between these two values as a function of population abundance relative to carrying capacity.

To examine the behavior of the stage-based model at intermediate abundances, we calculated the rate of increase, generation time and pregnancy rate for N/K equal to 0.5 and 0.85 (Table 5).

Table 5. Behavior of the model at intermediate abundances.

	N/K	
	0.5	0.85
Rate of increase (λ)	1.041	1.009
Generation time	18.0	19.2
Pregnancy rate	0.37	0.28
% lactating	0.10	0.075

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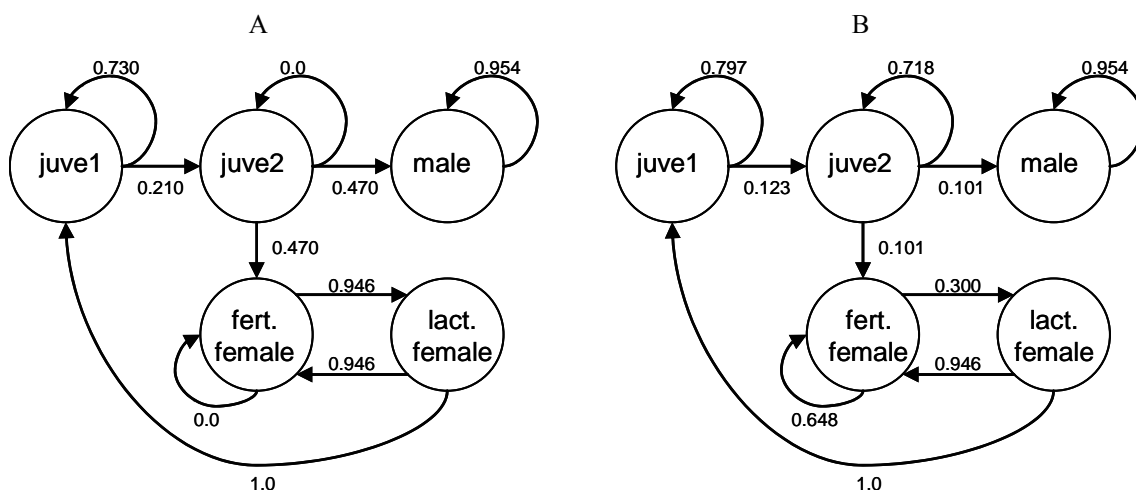
A

B

Figure 1. Life history diagrams illustrating the life stages and transition probabilities used in the model when the population is a) near zero density and b) near carrying capacity. Note that since growth/survival occurs before reproduction in METASIM, every individual in the lactating female class will have just given birth to a calf; thus, the birth rate for the lactating female class is 1.0. Stage abbreviations are juve1: first juvenile stage; juve2 – second juvenile stage; male – mature male; fert. female – fertile female; lact. femalae – lactating female.